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Biodemography and Genetics of the Berba of Benin

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KEY WORDS Biodemography, Genetic polymorphisms, Berba, African populations

ABSTRACT Genetic structure of the Berba of Benin was studied on the basis of biodemographic data and ABO, RH, MNS, KEL, JK, FY, ACP1, ADA, AK1, CA2, ESD, GLO1, G6PD, PGD, PGM1 (subtypes and thermostability), PGM2, PGP, SODA, HBα, HBβ, HBδ, BF, C3, and HP gene frequencies. Comparisons were carried out with other populations of Benin and of sub-Saharan Africa. Correspondence analysis revealed genetic differentiation among the three main groups of populations who inhabit sub-Saharan Africa: Bushmen–Hottentots, Pygmies, and Negroes. The genetic differentiation of the Negroes in relation to their linguistic affiliation and geographic localization was evident. The first group included the populations belonging to the Bantoid subfamily of the Nigritic linguistic stock living in southern Africa; in the second subcluster the populations of central–eastern Africa were localized, and the third subcluster included the populations living in the West. © 1996 Wiley-Liss, Inc.

The Berba population immigrated from Togo in northwestern Benin at an unknown time in the past. At present they live in the Materi district (10°40′ N, 1°04′ E; Fig. 1) of the Atacora province (Cornevin, 1962), and number about 10,000 individuals (Kouandété, 1971; Recensement general de la population et de l'habitation: Mars 1979, 1983). According to Greenberg (1955, 1970) they belong to the Gur subfamily of the Niger–Congo linguistic family, which Murdock (1959) renamed as the Voltaic subfamily of the Nigritic linguistic stock. They are mainly animistic in religion, though Christianity and Islam are also practiced. Most of the Berba reside in villages scattered in parkland savanna; the climate is tropical wet–dry (Köppen's classification; New Encyclopaedia Britannica, 1991), and the annual temperature averages about 13°C–40°C in the dry season (November–March) and about 25°C–40°C in the rainy season (April–October), with little seasonal variation. Rainfall averages between 800 and 900 mm per year, concentrated in the rainy season (Adam and Boko, 1983).

These people cultivate all the Sudanic plants, especially millet and sorghum, and plants of other origin such as melons and onions from southwest Asia; bananas, cucumbers, eggplants, rice, taro, and yams from southeast Asia; and beans, maize, manioc, papayas, peanuts, peppers, squash, sweet potatoes, tobacco, and tomatoes from the Americas. Other plants are commonly

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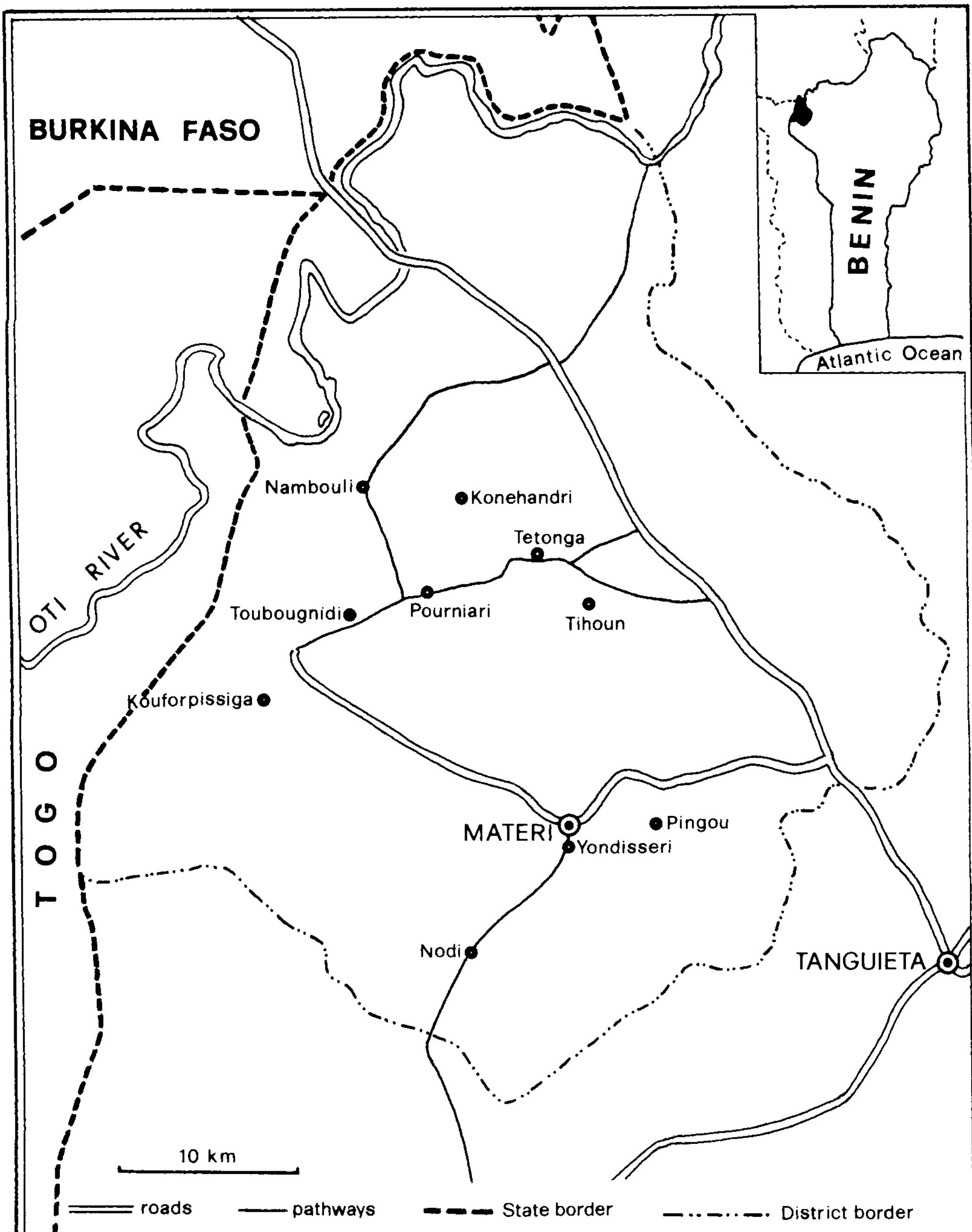

Fig. 1. Map of the examined area.

present in their diet: amaranth, bitter leaf, baobab, and okra. The agricultural technique is alternating hoe cultivation with crop rotation and fallowing. They practice hunting in the dry season; they occasionally fish in the rainy season, and gather to supplement their diet. They breed mainly a few humpless short-horned cattle, and keep

sheep, dogs, chickens, horses, and pigs as well. Cow, sheep, dog, and game meat is eaten exclusively during ceremonies such as marriages, funerals, and circumcision (which marks the end of childhood). Cows and sheep are also sold to make the money needed to buy goods for preparing these ceremonies or for other special occasions. The men hunt and fish; the women engage in trade, carry water, and cook, while gathering is done by both sexes. The bulk of agricultural work is done mainly by the men, while the women render considerable assistance in the fields. The children usually help with cattle-herding, which is done mostly by the men.

The traditional and predominant type of habitation is a round hut with mud walls or sun-dried bricks and a straw conical roof. The huts are grouped in circular walled compounds that set the boundaries of the property area belonging to each family. Each hut is used for a particular need: sleeping area, stable, storage area, etc. A more modern type of habitation consists of a large rectangular single-room house.

Recent surveys have revealed that there is apparent nutritional stress and consistent disease stress on children. In fact, intestinal parasites and avitaminosis A are common, affecting 27% and 8% of the children, respectively. Falciparum malaria is endemic; 30% of the children and 12% of the adults are infected with it. Water is supplied mostly (90%) by contaminated wells or water courses (Adandedjan et al., 1989; Cresta and Biondi, 1991).

The traditional Berba matrimonial pattern largely permits polygyny. Exchange marriages are arranged by the heads of the families. That means that the groom is obliged to give to his bride's family a woman of his own family. If there is no woman available to exchange, it is common to look for a bride in another tribe. In this case, the groom has to pay a bride price. The oldest members of each village play an important role in the organization of social life; traditional medicine is handed on from father to son, but those who practice it are not considered medicine men.

According to Cornevin (1962), the Berba are included in the Paragourma peoples who live in the north and central areas together with the groups of "Mossi" culture and language; the tribes who belong to the Grossi group; and the Dendi, the Peuls, the Bariba, the Guin, the Basseda, and the Gouang. The south is settled by the large cultural group of the Fon-Adja, the Yoruba, and the small group of the Hollidjé, nowadays included in the Yoruba.

In order to define the genetic makeup of the Berba, in 1988 we started an anthropological survey of 10 Berba villages. In this paper we analyze the demographic and genetic structure of this population group as well as their genetic relationships with the other populations of Benin and of sub-Saharan Africa.

MATERIALS AND METHODS

Demographic data were collected through interviews with 247 families coming from 10 Berba villages of the Materi district. Data on pregnancies, births, and living children of 314 women older than 45 years were collected at "Fatebenefratelli" Hospital in Tanguietà, the chief town of the Atacora province (see Fig. 1). These data are fairly representative of the whole Berba population since "Fatebenefratelli" is the only hospital in north Benin, and it is visited by all the peoples from this area irrespective of their economic and ethnic status.

A total of 285 unrelated and apparently healthy adults of both sexes, with both parents belonging to the Berba ethnic group and coming from the same villages where the demographic data collection was carried out, were tested for ABO, Rhesus (RH), MNSs (MNS), Kell (KEL), Kidd (JK), and Duffy (FY) blood groups; acid phosphatase 1 (ACP1), adenosine deaminase (ADA), adenylate kinase 1 (AK1), carbonic anhydrase II (CA2), esterase D (ESD), glyoxalase 1 (GLO1), glucose-6-phosphate dehydrogenase (G6PD), phosphogluconate dehydrogenase (PGD), phosphoglucomutase 1 (PGM1) subtypes and thermostability, phosphoglucomutase 2 (PGM2), phosphoglycollate phosphatase (PGP), and superoxide dismutase A (SODA) red cell enzymes; hemoglobin (HBα, β, and δ); and properdin factor B (BF), complement component-3 (C3), and haptoglobin

(HP) serum proteins. Blood specimens were withdrawn by venipuncture. Each sample was fractionated into two sterile tubes, one without any anticoagulant and the other one with ACD. The tubes were kept at 4–6°C for no longer than 10 days until they could be taken to the universities of Rome and L'Aquila for analysis. The following techniques were used for blood groups: ABO, agglutination in saline solution by anti-A, -B, -A + B, -A1, and -H sera for antigens, and ABO erythrocyte test for antibodies; MNS, agglutination in saline solution by anti-M, -N, and -S sera, and by anti-globulin technique for s antigen; RH, agglutination in saline solution at 37°C by anti-C, -c, -D, -E, and -e sera. The investigation of D antigen was also performed by an incomplete anti-D hemodiagnostic serum by anti-globulin test; KEL, agglutination in saline solution by anti-K and -k sera; JK, agglutination in saline solution by anti-JKa and -JKb sera; and FY, agglutination in saline solution by anti-Fya and -Fyb sera. The maximum-likelihood method was used to calculate gene frequencies. Red cell lysates were carried out according to the standard technique and stored at −80°C pending analysis. Electrophoretic separation of ACP1, ADA, AK1, CA2, ESD, GLO1, G6PD, PGD, PGM2, and SODA was performed on cellulose acetate strips (Cellogel, Chemetron Labometrics, Milan, Italy) following Spielmann and Kühnl (1982) for AK1, Noppinger and Morrison (1981) for CA2, Meera Khan and Doppert (1976) for GLO1, W.H.O. guidelines (Betke et al., 1967) for G6PD, and according to the methods listed in the handbook by Harris and Hopkinson (1976), modified by Chemetron Labometrics, for ACP1, ADA, ESD, PGD, PGM2, and SODA; PGP was typed on starch gel following the methods of Barker and Hopkinson (1978); HB was typed on cellulose acetate strips (Helena Laboratories, Beaumont, TX) following Golias (1971); the IEF for PGM1 subtypes was carried out on PAG employing the methods of Kühnl and Spielmann (1978), with minor modification; and the PGM1 thermostability phenotypes were determined by combining the IEF procedure with the heat denaturation technique as described by Scozzari et al. (1981). BF and C3 were typed on cellulose acetate by immunofixation following the methods of Germenis et al. (1982), and Gruppioni et al. (1993); HP was analyzed on polyacrylamide gel following Grunbaum (1981).

Correspondence analysis (Benzécri, 1973; Greenacre, 1984; Lebart et al., 1984) was applied to study the genetic relationships between the Berba and the other populations of sub-Saharan Africa. It was carried out using the procedures CORRESP and MXPLOT of the NTSYS-pc package (Rohlf, 1988). This statistical technique provides the graphical representation of the populations and markers on a plane, as well as analytical data, i.e., the relative and absolute contributions, which help explain the plotting obtained. The absolute contributions express the portion of variability that can be attributed to each single element, either a population or gene frequency, within the variability explained by a factor, and the relative contributions indicate the portion of variability that can be attributed to each factor in the explanation of the variability of an element, i.e., the goodness of the representation of each element on the axes.

RESULTS AND DISCUSSION

Demographic data

Age and sex distribution shows an excess of females in the second class (Table 1). This finding is in line with the data available for the Atacora province (sex ratio = 80) as well as for the whole country (sex ratio = 76), and it is mainly due to the extensive emigration of males aged between 20 and 30 (Recensement general de la population et de l'habitation: Mars 1979, 1987). In addition, polygyny could be a further reason for such an excess. The lack of females in the youngest and oldest age intervals could be attributed to the exchange marriage practice and the high rate of deaths during childbirth. The overall sex ratio obtained is 98, and the estimated average age 21 years.

The differences in marriage behavior (Table 2) in relation to male age appear to be statistically significant ($0.05 > P > 0.02$, 6 d.f.). In fact, monogamy is quite common among males of the youngest age class, whereas the males of the second age class practise polygyny more frequently than ex-

TABLE 1. Age and sex distribution in the Berba

Sex	Age interval (years)			Estimated average age in years (mean ± SD)
	0–15	16–45	>45	
Males	409	272	101	21 ± 20
%	52.3	34.8	12.9	
Females	359	365	72	20 ± 17
%	45.1	45.9	9.0	
Total	768	637	173	21 ± 18
%	48.7	40.3	11.0	
Sex ratio	114	75	140	

TABLE 2. Monogamy and polygyny in the Berba

Number of wives	Male age distribution		
	20–40	41–60	>60
1	84	47	25
	(73.2)[1]	(55.8)	(27.0)
2	26	28	15
	(32.4)	(24.7)	(11.9)
3	3	8	2
	(6.1)	(4.6)	(2.3)
4	1	4	0
	(2.3)	(1.8)	(0.9)

[1] Expected frequencies are reported in parentheses.

TABLE 3. Ethnic marriage structure in the Berba

Type of marriage	n	%
Male Berba × female Berba	328	90.9
Male Berba × female non-Berba	12	3.3
Male non-Berba × female Berba	15	4.1
Male non-Berba × female non-Berba	6	1.7
Total	361	

TABLE 4. Marriage movements in the Berba

Partners' birthplace	n	%
Same village	56	15.8
Two different villages in the Materi district	267	75.4
Two different villages in the Atacora province	13	3.7
At least one village outside the province	18	5.1
Total	354	

pected. Notwithstanding this polygyny, their genetic contribution to the population is nondisproportionate since about 60% of the families with at least one child are monogamic. As reported in Table 3, 91% of the mating occurred between persons who identified themselves as Berba (ethnic endogamy); exogamy (7.4%) is equally distributed between the sexes. The percentage of non-Berba people in the Berba community is very small (1.7%), which underlines the high current isolation of this population. As regards marriage migration (Table 4), the Berba are characterized by a very high frequency of village exogamy, with about 71% of the unions having partners born in different villages.

The mean values of pregnancies (8.8) and births (8.1) obtained from the sample of 314 women older than 45 do not show statistically significant differences; this indicates a very low incidence of miscarriages. Obviously this observation does not take into account the miscarriages that occur during the earliest stages of pregnancy. On the other hand, the number of living offspring (4.3) is only half that of the births, reflecting the high degree of environmental stress to which the Berba are exposed (Morana et al., 1989).

Genetic data

The distribution of the phenotype and allele frequencies for the polymorphic markers is given in Table 5. Three of these distributions disagree with the Hardy–Weinberg equilibrium: ABO and BF at the 0.05 level, and MNS at the 0.001 (due to the MN locus only). Variant phenotypes were detected at ACP1, G6PD, and C3 loci. The two ACP1 variants showed a similar electrophoretic pattern characterized by two bands with an electrophoretic mobility slower than ACP1*B products, and probably corresponding to the products of ACP1*D allele (Karp and Sutton, 1967), together with the bands characteristic of the A type. The G6PD variant showed a normal activity and an electrophoretic mobility slower (90%) than that of the B type. The presence of four females (out of the 171 tested) heterozygous for the same variant (two individuals), or for another slow variant (93%) with normal activity, confirms the high degree of heterogeneity of this locus (Luzzatto and Battistuzzi, 1985; Rickards et

TABLE 5. Phenotype and gene frequencies of the polymorphic markers in the Berba population

Systems	Phenotypes	Observed frequencies	Expected frequencies	Alleles or haplotypes	Frequencies ± 1 SE
ABO[1]	A1	43	34.6	A1	0.086 ± 0.012
	Ai	2	1.9	Ai	0.005 ± 0.003
	A2	8	8.1	A2	0.021 ± 0.006
	B	102	96.9	B	0.220 ± 0.017
	A1Ai	0	0.2	O	0.668 ± 0.020
	A1A2	0	1.0		
	A1B	3	10.7		
	A2Ai	0	0.1		
	AiB	1	0.6		
	A2B	4	2.6		
	O	120	126.3		
	Total	283			
G^2 (H.W.) = 9.6, d.f. = 3, $0.025 > P > 0.01$ (Ai, A1Ai, A1A2, and A2Ai phenotypes were pooled)					
FY[1]	FY (a+b+)	2	0.1	FY*a	0.014 ± 0.005
	FY (a+b−)	6	7.8	FY*b	0.018 ± 0.006
	FY (a−b+)	8	9.8	FY	0.968 ± 0.007
	FY (a−b−)	267	265.3		
	Total	283			
JK[1]	JK (a+b−)	176	170.8	JK*b	0.223 ± 0.017
	JK (a+b+)	88	98.1		
	JK (a−b+)	19	14.1		
	Total	283			
G^2 (H.W.) = 2.9, d.f. = 1, $P > 0.05$					
KEL[1]	KK	0		KEL*K	0.002 ± 0.002
	Kk	1			
	kk	282			
	Total	283			
MNS[1]	MS	3	4.5	MS	0.126 ± 0.014
	MSs	40	30.3	Ms	0.425 ± 0.021
	Ms	61	51.3	NS	0.120 ± 0.014
	MNS	9	8.5	Ns	0.329 ± 0.020
	MNSs	36	52.2		
	MNs	59	79.2		
	NS	8	4.1		
	NSs	23	22.3		
	Ns	44	30.6		
	Total	283			
G^2 (H.W.) = 24.6, d.f. = 5, $P < 0.001$					
RH[1]	CDE	0	0.0	CDE	0.012 ± 0.005
	CDEe	0	0.5	CDe	0.061 ± 0.010
	CDe	1	1.5	Cde	0.014 ± 0.005
	Cde	0	0.1	cDE	0.071 ± 0.011
	CcDE	1	1.1	cDe	0.605 ± 0.021
	CcDEe	9	8.8	cde	0.237 ± 0.018
	CcDe	35	33.6		
	Ccde	2	1.8		
	cDE	3	1.4		
	cDEe	30	33.6		
	cDe	186	184.8		
	cde	16	15.8		
	Total	283			
G^2 (H.W.) = 2.1, d.f. = 2, $P > 0.25$ (CDE, CDEe, CDe, Cde, and CcDE phenotypes were pooled)					
ACP1	A	15	12.2	ACP1*A	0.211 ± 0.017
	AB	87	91.6	ACP1*B	0.772 ± 0.018
	B	173	171.3	ACP1*R	0.014 ± 0.005
	AR	1	1.6		
	BR	7	6.2		
	R	0	0.1		
	A-var	2			
	Total	285			
X^2 (H.W.) = 1.3, d.f. = 2, $P > 0.25$ (the χ^2 was calculated on 283 subjects, i.e., excluding the two variant phenotypes; AR and R phenotypes were pooled)					
ADA	1	276		ADA*5	0.014 ± 0.005
	51	8			
	Total	284			
CA2	1	207	208.1	CA2*2	0.144 ± 0.015
	21	72	70.0		
	2	5	5.9		
	Total	284			

(continued)

TABLE 5. (Continued)

Systems	Phenotypes	Observed frequencies	Expected frequencies	Alleles or haplotypes	Frequencies ± 1 SE
X^2 (H.W.) = 0.2, d.f. = 1, $P > 0.50$					
ESD	1	260	257.7	ESD*2	0.049 ± 0.009
	21	22	26.6		
	2	3	0.7		
	Total	285			
GLO1	1	35	27.7	GLO1*1	0.312 ± 0.019
	21	108	122.4		
	2	142	134.9		
	Total	285			
X^2 (H.W.) = 4.0, d.f. = 1, $0.05 > P > 0.025$					
G6PD[2]	A	31		GD*A	0.272 ± 0.042
	B	64		GD*B	0.561 ± 0.046
	A-	18		GD*A-	0.158 ± 0.034
	var	1			
	Total	114			
PGD	A	238	239.1	PGD*C	0.084 ± 0.012
	AC	46	43.9		
	C	1	2.0		
	Total	285			
X^2 (H.W.) = 0.6, d.f. = 1, $P > 0.25$					
PGM1	1A	176	169.7	PGM1*1A	0.773 ± 0.018
	1A2A	52	56.6	PGM1*2A	0.129 ± 0.014
	2A	5	4.7	PGM1*1B	0.079 ± 0.011
	1A1B	27	34.7	PGM1*2B	0.019 ± 0.006
	1B	3	1.8		
	1A2B	8	8.3		
	2A1B	10	5.8		
	2A2B	1	1.4		
	1B2B	2	0.9		
	2B	0	0.1		
	Total	284			
X^2 (H.W.) = 6.2, d.f. = 3, $P = 0.10$ (1B, 2A2B, 1B2B, and 2B phenotypes were pooled)					
HBβ[3]	A	181	185.2	HBβ*A	0.806 ± 0.017
	AC	71	67.5	HBβ*C	0.147 ± 0.015
	AS	26	21.6	HBβ*S	0.047 ± 0.009
	C	6	6.2		
	CS	1	3.9		
	S	0	0.6		
	Total	285			
X^2 (H.W.) = 3.9, d.f. = 2, $P > 0.10$ (CS and S phenotypes were pooled)					
BF	F	78	69.4	BF*F	0.554 ± 0.023
	FS	82	97.4	BF*S	0.389 ± 0.023
	S	42	34.2	BF*F1	0.044 ± 0.010
	FF1	10	11.0	BF*S1	0.013 ± 0.005
	SF1	6	7.7		
	FS1	2	3.3		
	SS1	4	2.3		
	F1S1	0	0.3		
	F1	2	0.4		
	S1	0	0.0		
	Total	226			
X^2 (H.W.) = 9.3, d.f. = 3, $0.05 > P > 0.025$ (SS1, F1S1, F1, and S1 phenotypes were pooled)					
C3	S	199	197.1	C3*F	0.064 ± 0.011
	FS	23	27.0		
	F	3	0.9		
	S-Svar	2			
	S-Fvar	1			
	Total	228			
HP	1	103	105.3	HP*2	0.269 ± 0.022
	21	82	77.5		
	2	12	14.2		
	0	33			
	Total	230			
X^2 (H.W.) = 0.7, d.f. = 1, $P > 0.30$ (the gene frequencies and χ^2 were calculated on 197 subjects, i.e., excluding the 0 phenotypes)					

[1] Preliminary data were reported in Biondi et al. (1991).
[2] Only males were examined.
[3] Preliminary data were reported in Biondi et al. (1989).

al., 1988; Calabrò et al., 1990; Vulliamy et al., 1991; Calabrò et al., 1993). The two C3 heterozygous variants displayed the S component with a band slower than the S type in one case and a band faster than the F type in the other case. AK1, PGM2, PGP, SODA, HBα, and δ loci were found to be monomorphic, as has already been found in other sub-Saharan African populations (Roychoudhury and Nei, 1988). PGM1 thermostability, studied for the first time in sub-Saharan Africa, also showed no variation.

To evaluate the genetic relationships between the Berba and the other populations of Benin, we collected from the literature data on the genetic markers studied in this survey. Excluding the HBβ locus, only few data are available. Comparisons were carried out excluding the samples labeled as "South" and "North" in the appendixes, which comprise mixed populations. As far as β-globin allele frequencies are concerned (Appendix A), the Berba and the other northern populations are characterized by high frequencies of HBβ*C allele (about 14%), and low values of HBβ*S (about 5%). These figures are typical of the populations who belong to the Gur or Voltaic peoples inhabiting the area included in the great bend of the Niger river (Livingstone, 1985). It seems that the HBβ*C allele probably originated in this region and from here spread over the surrounding populations (Rucknagel and Neel, 1961; Livingstone, 1967; Cavalli-Sforza and Bodmer, 1971). An opposite pattern of HBβ*C and HBβ*S allele frequencies distribution characterizes southern Benin (about 4% and 12%, respectively). This agrees with the presence of a negative correlation between the two alleles (Rucknagel and Neel, 1961; Allison, 1964). G6PD deficiency (Appendix B) shows a homogeneous distribution in the populations of Benin. This is in line with the presence of malarial morbidity both in the northern (about 30%; Biondi et al., 1989) and the southern (about 20%; Djivoh et al., 1988) areas of the country. ABO and MNS systems (Appendix C) show highly significant heterogeneity ($P < 0.001$) among populations. The heterogeneity found in the MNS system is due to Ss ($P < 0.001$). The analysis considering only the MN locus, for which more data are available, did not show any significant difference. Among the other polymorphic markers (Appendix D), only the ACP1 and PGM1 (subtyping) systems display statistically significant differences ($P < 0.001$). However, unlike that at the HBβ locus, this heterogeneity is not due to a genetic differentiation between northern and southern groups.

In the subsequent step we applied correspondence analysis to study the genetic relationships between the Berba and the other populations of sub-Saharan Africa for which data on the genetic markers analyzed in the present paper were available. We reached a total of 22 alleles and haplotypes, and 20 populations, which belong to four of the 11 linguistic stocks proposed by Murdock (1959) for Africa (Appendix E). Figure 2 displays the two-dimensional plot of the first two axes, which account for 57.1% of the total variability; in Tables 6 and 7 absolute and relative contributions for the same axes are reported. Three main groups are unambiguously distinguishable (see Table 6): Pygmies, Khoisans (Bushmen and Hottentots), and all other populations, hereinafter referred to as Negroes. Closely grouped together, the four Bushmen populations cluster with the Nama, the only Hottentot population included in the analysis. However, unlike the results obtained by Harpending and Jenkins (1973) for some southern African populations, our analysis does suggest that some degree of difference between the Bushmen and Hottentots might exist. The Negroes also form a tight cluster, and the Babinga, the Pygmy group living in the Central African Republic, appear sharply differentiated, largely along the second axis. The two alleles that mostly contribute (see Table 7) to the observed pattern of distribution are PGM2*6, unique to the Pygmy populations, and ACP1*R, which reaches high frequencies both in the Khoisans and the Pygmies (see Appendix E). The same clustering of the African Black populations was obtained by Nei and Roychoudhury (1982) by means of genetic distance and cluster analysis.

The projection of the Negroes on the first axis provides good, dependable evidence of the genetic differentiation of these populations in relation to their linguistic affiliation

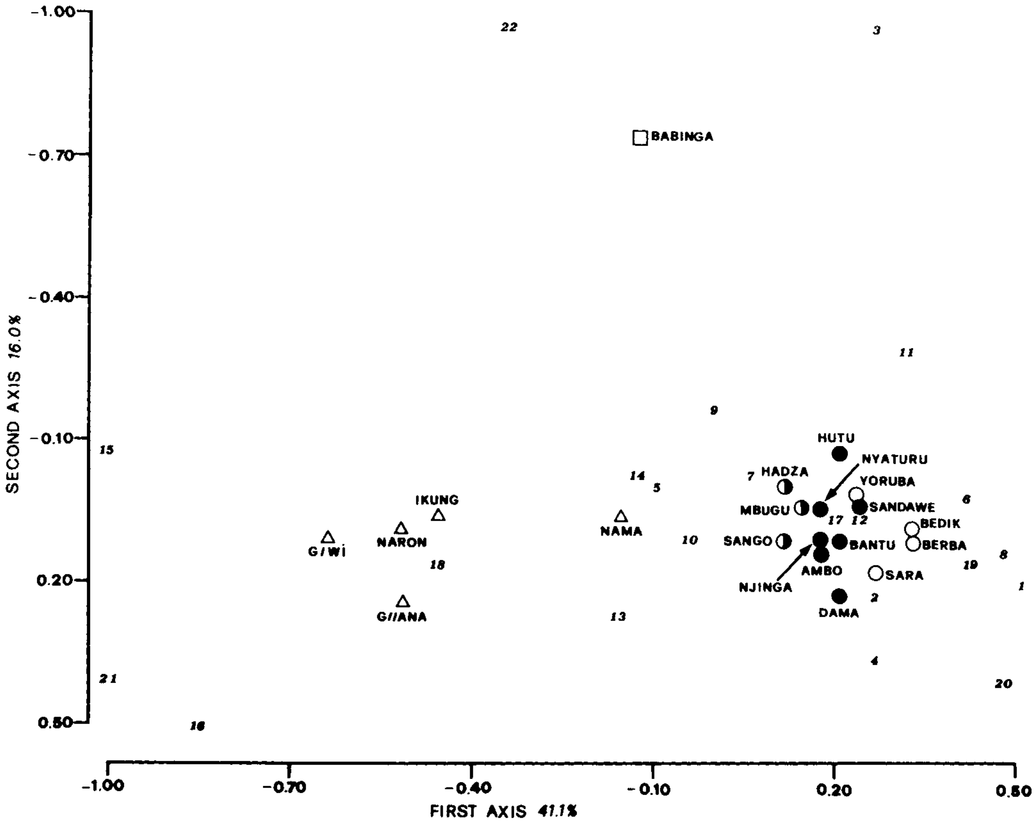

Fig. 2. Two-dimensional correspondence analysis of 20 populations of sub-Saharan Africa, and 22 alleles or haplotypes. Triangles indicate Bushmen and Hottentot groups; square indicates the Pygmy population; circles indicate the Negroes (half open/half full circles = Eastern populations, full circles = Southern populations, and open circles = Western populations). Numbers indicate the position of the markers on the plane: 1 = CDE, 2 = CDe, 3 = Cde, 4 = cDE, 5 = cDe, 6 = cde, 7 = ABO*A, 8 = ABO*B, 9 = MS, 10 = Ms, 11 = NS, 12 = HP*1, 13 = ACP1*A, 14 = ACP1*C, 15 = ACP1*R, 16 = AK1*2, 17 = PGM1*2, 18 = PGM1*6, 19 = PGD*C, 20 = PGD*R, 21 = PGM2*2, 22 = PGM2*6.

and geographic localization. All the populations belonging to the Bantoid subfamily of the Nigritic linguistic stock and geographically located in the southern regions of the continent group together in the middle of the dispersion. On the left side of this cluster are the three populations living in central–eastern Africa: the Mbugu and the Hadza of the Hamitic stock, and the Sango of the eastern subfamily of the Nigritic stock. It is noticeable, however, that the Hadza are not well represented in the plane defined by the first two axes, the sum of their relative contributions being only about 5% (Table 6). On the right side of the projection, the groups living in the west are gathered. This subcluster includes, besides the Berba, the Bedik of the Atlantic and the Yoruba of the Kwa subfamilies of the Nigritic stock, and the Sara, the only population of Sudanic language affiliation. The Sandawe of southern Tanzania, who have close linguistic affinities to the Khoisans, appear spatially located between the nearby southern populations and the western cluster, confirming that they are genetically similar to the other Negroes. The pattern of distribution of the populations along the third axis, which explains 8.8% of the residual variability, does not substantially alter the plot shown in Figure 2. Only the Hadza of Tanzania, in this case better represented (the relative contribution of the

TABLE 6. Absolute and relative contributions of the 20 populations to the first two axes

Populations	Contributions: Absolute I axis	Absolute II axis	Relative I axis	Relative II axis
Nharon	0.159740	0.002488	0.857152	0.005218
Nama	0.021882	0.000877	0.136628	0.002140
G/wi	0.256097	0.004289	0.921979	0.006035
G//ana	0.162852	0.063873	0.600404	0.092041
!Kung	0.108931	0.000209	0.733609	0.000549
Bantu	0.016548	0.004992	0.237541	0.028007
Yoruba	0.021388	0.001009	0.265746	0.004900
Njinga	0.012777	0.004509	0.195341	0.026945
Ambo	0.012331	0.009898	0.213768	0.067067
Bedik	0.051289	0.001378	0.590032	0.006194
Sandawe	0.020510	0.000342	0.309066	0.002017
Nyaturu	0.012262	0.000012	0.407141	0.000159
Hadza	0.003915	0.005647	0.033260	0.018751
Dama	0.017600	0.039653	0.131612	0.115899
Mbugu	0.006921	0.000067	0.179094	0.000682
Babinga	0.011207	0.810799	0.032169	0.909697
Hutu	0.017256	0.021606	0.255788	0.125182
Sara	0.028965	0.021895	0.314775	0.093002
Berba	0.052615	0.001387	0.502334	0.005177
Sango	0.004915	0.005069	0.163218	0.065799

TABLE 7. Absolute and relative contributions of the 22 alleles or haplotypes to the first two axes

Alleles or haplotypes	Contributions: Absolute I axis	Absolute II axis	Relative I axis	Relative II axis
CDE	0.002495	0.000169	0.074196	0.001962
CDe	0.008060	0.011929	0.113488	0.065650
Cde	0.001087	0.126562	0.010642	0.484298
cDE	0.010413	0.055052	0.124084	0.256418
cDe	0.046409	0.013767	0.688362	0.079811
cde	0.074144	0.002229	0.517264	0.006079
ABO*A	0.000052	0.011407	0.000526	0.045071
ABO*B	0.089728	0.007171	0.543470	0.016977
MS	0.000971	0.057617	0.008572	0.198870
Ms	0.010031	0.017154	0.298157	0.199285
NS	0.023569	0.085827	0.243861	0.347082
HP*1	0.082097	0.002691	0.747536	0.009576
ACP1*A	0.029277	0.089845	0.277699	0.333091
ACP1*C	0.000263	0.000113	0.008922	0.001497
ACP1*R	0.455856	0.010251	0.924110	0.008122
AK1*2	0.061242	0.039806	0.465591	0.118283
PGM1*2	0.017856	0.000562	0.257388	0.003166
PGM1*6	0.001825	0.000186	0.020679	0.000824
PGD*C	0.019668	0.003183	0.237568	0.015025
PGD*R	0.000884	0.001572	0.037201	0.025840
PGM2*2	0.062360	0.015561	0.676146	0.065945
PGM2*6	0.001712	0.447349	0.008626	0.880924

third axis equals 52%), appear to be genetically more distant from the two populations living in the Central African Republic, the Mbugu of the same linguistic affiliation and the Sango (data not shown).

On the whole, the genetic picture obtained may very well reflect the expansion of the Bantu-speaking peoples, the major Iron Age movement within Africa. This spread was due to a population explosion that started about 200 BC and led to the outpouring of Negroes from the Cameroon area over most of the continent south of the equator by the 7th century AD. As a consequence, the predominance of such earlier-established groups as the Pygmies and Bushmen declined, forcing the former to migrate to the inner parts of the central African forest and the latter to retreat to the south. The causes and the exact routes of the Bantu expansions have been extensively investigated by many scholars, and the most widely held view is that their itinerary lay eastward across the southern Sudan to the Indian Ocean first, and afterwards south, past the great lakes of the northeast (McEvedy, 1980).

Although the scarcity of data available limited the number of the populations considered, the pattern of distribution of the sub-Saharan African populations that we obtained is in line with the results reported by Excoffier et al. (1987) on the basis of Rhesus, Gm, and HLA systems, and by Tartaglia and Rickards (1994) on the basis of PGM1 subtypes distribution. The results of our study underpin the greater genetic affinities between populations geographically related than between those linguistically grouped; this stresses once more that also for this part of the world, the unambiguous reconstruction of the microevolutionary history of human populations must be based on the study of the complex network of historical events, cultural characteristics, and geographical patterns which have determined all phases of human evolution.

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*APPENDIX A. HBβ*C and HBβ*S allele frequencies in Benin*

Populations	N	Frequencies ± 1 SE		References[3]
		HBβ*C	HBβ*S	
Northern populations				
Bariba	147	0.092 ± 0.017	0.034 ± 0.011	1
Bariba	50	0.110 ± 0.031	0.070 ± 0.025	9
Total Bariba	197	0.097 ± 0.015	0.043 ± 0.010	
Berba	1258	0.160 ± 0.007	0.047 ± 0.004	2
Berba	395	0.151 ± 0.013	0.047 ± 0.008	5
Berba	285	0.147 ± 0.015	0.047 ± 0.008	ps
Total Berba	1938	0.156 ± 0.006	0.047 ± 0.003	
Dendi	50	0.080 ± 0.027	0.080 ± 0.027	9
Somba	1381	0.130 ± 0.006	0.059 ± 0.004	1
North[2]	55	0.145 ± 0.034	0.055 ± 0.022	1
North	255	0.141 ± 0.015	0.057 ± 0.010	3
Southern populations				
Djedje	52	0.038 ± 0.019	0.077 ± 0.026	7
Fon	247	0.018 ± 0.006	0.162 ± 0.017	4
Fon	77	0.045 ± 0.017	0.110 ± 0.025	7
Fon	54	0.019 ± 0.013	0.139 ± 0.033	8
Fon	20	0.050 ± 0.034	0.100 ± 0.047	3
Total Fon	398	0.025 ± 0.006	0.146 ± 0.013	
Goun	157	0.025 ± 0.009	0.124 ± 0.019	7
Goun	229	0.039 ± 0.009	0.083 ± 0.013	8
Total Goun	386	0.033 ± 0.006	0.100 ± 0.011	
Nago	77	0.045 ± 0.017	0.117 ± 0.026	7
Nago	46	0.022 ± 0.015	0.109 ± 0.032	8
Total Nago	123	0.036 ± 0.012	0.114 ± 0.020	
Tofinu	102	0.054 ± 0.016	0.098 ± 0.021	7
South[1]	377	0.038 ± 0.007	0.107 ± 0.011	6
South	394	0.036 ± 0.007	0.112 ± 0.011	6
South	365	0.057 ± 0.009	0.119 ± 0.012	1
South	469	0.036 ± 0.006	0.096 ± 0.010	8

[1] South: these samples include individuals of different populations of southern Benin.
[2] North: these samples include individuals of different populations of northern Benin.
[3] ps: present study; 1: Biondi et al., 1980; 2: Biondi et al., 1989; 3: unpublished data (North: A = 163, AC = 56, AS = 27, C = 7, CS = 2, S = 0; Fon: A = 15, AC = 1, AS = 3, C = 0, CS = 1, S = 0); 4: Cresta et al., 1968; 5: Morana et al., 1989; 6: Spedini et al., 1973; 7: Spedini et al., 1980; 8: Spedini et al., 1981b; 9: Rickards and Martínez-Labarga, 1994.

APPENDIX B. G6PD deficiency distribution in Beninese males

Populations	N	Frequencies ± 1 SE	References[2]
Northern populations			
Bariba	36	0.139 ± 0.058	4
Berba	114	0.158 ± 0.034	ps
Dendi	37	0.189 ± 0.064	4
Southern populations			
Fon	315	0.190 ± 0.022	1
Fon	36	0.139 ± 0.058	4
Total Fon	351	0.185 ± 0.021	
South[1]	278	0.158 ± 0.022	2
South	215	0.126 ± 0.023	3

[1] South: these samples include individuals of different populations of southern Benin.
[2] ps: present study; 1: Cresta et al., 1968; 2: Spedini et al., 1973; 3: Spedini et al., 1981b; 4: Rickards and Martínez-Labarga, 1994.

APPENDIX C. Blood group alleles and haplotype frequencies in Benin

Populations and systems	N	Alleles and haplotypes frequencies ± 1 SE						References[2]
ABO		A	B	O				
Northern populations								
Berba	283	0.112 ± 0.013	0.220 ± 0.017	0.668 ± 0.020				ps
Southern populations								
Fon	375	0.146 ± 0.013	0.139 ± 0.013	0.715 ± 0.016				1
Fon	54	0.140 ± 0.033	0.173 ± 0.036	0.687 ± 0.045				3
Total Fon	429	0.145 ± 0.012	0.143 ± 0.012	0.712 ± 0.015				
Goun	229	0.143 ± 0.016	0.103 ± 0.014	0.754 ± 0.020				3
Nago	46	0.220 ± 0.043	0.167 ± 0.039	0.613 ± 0.051				3
South[1]	210	0.108 ± 0.015	0.167 ± 0.018	0.725 ± 0.022				2
MNSs		MS	Ms	NS	Ns			
Northern populations								
Berba	283	0.126 ± 0.014	0.425 ± 0.021	0.120 ± 0.014	0.329 ± 0.020			ps
Southern populations								
Fon	367	0.039 ± 0.007	0.535 ± 0.018	0.037 ± 0.007	0.389 ± 0.018			1
MN		M	N					
Northern populations								
Berba	283	0.551	0.449 ± 0.021					
Southern populations								
Fon	367	0.573	0.427 ± 0.018					1
Fon	54	0.519	0.481 ± 0.048					3
Total Fon	421	0.566	0.434 ± 0.017					
Goun	229	0.609	0.391 ± 0.023					3
Nago	46	0.544	0.456 ± 0.052					3
South	340	0.535	0.465 ± 0.019					2
Rhesus		CDE	CDe	Cde	cDE	cDe	cde	
Northern populations								
Berba	283	0.012 ± 0.005	0.061 ± 0.010	0.014 ± 0.005	0.071 ± 0.011	0.605 ± 0.021	0.237 ± 0.018	ps
Southern populations								
South	398		0.117 ± 0.011	0.016 ± 0.004	0.074 ± 0.009	0.642 ± 0.017	0.151 ± 0.013	2
Kell		KEL*K	KEL*k					
Northern populations								
Berba	283	0.002 ± 0.002	0.998					ps
Southern populations								
Fon	319	1.000						1

[1] South: these samples include individuals of different populations of southern Benin.
[2] ps: present study; 1: Spedini and Cresta, 1968; 2: Spedini et al., 1973; 3: Spedini et al., 1981b.

APPENDIX D. Red cell enzyme and serum protein allele frequencies in Benin

Populations and systems	N	Allele frequencies ± 1 SE				References[2]
ACP1		ACP1*A	ACP1*B	ACP1*R	ACP1*C	
Northern populations						
Bariba	50	0.080 ± 0.027	0.920			5
Berba	285	0.211 ± 0.017	0.772 ± 0.018	0.014 ± 0.005		ps
Dendi	50	0.080 ± 0.027	0.850 ± 0.036	0.070 ± 0.025		5
Southern populations						
Djedje	46	0.185 ± 0.040	0.783 ± 0.043	0.032 ± 0.018		2
Fon	38	0.145 ± 0.040	0.763 ± 0.049	0.053 ± 0.026	0.039 ± 0.022	2
Fon	50	0.040 ± 0.019	0.950 ± 0.022	0.010 ± 0.009		5
Total Fon	88	0.085 ± 0.021	0.869 ± 0.025	0.029 ± 0.013	0.017 ± 0.010	
Goun	122	0.164 ± 0.024	0.783 ± 0.026	0.053 ± 0.014		2
Nago	45	0.111 ± 0.033	0.856 ± 0.037	0.022 ± 0.015	0.011 ± 0.011	2
Tofinu	102	0.186 ± 0.027	0.760 ± 0.030	0.054 ± 0.016		2
South[1]	295	0.158 ± 0.015	0.790 ± 0.017	0.035 ± 0.008	0.017 ± 0.005	1
South	104	0.260 ± 0.030	0.692 ± 0.032	0.048 ± 0.015		3
ADA		ADA*1	ADA*5	ADA*2		
Northern populations						
Bariba	50	0.980	0.020 ± 0.014			5
Berba	284	0.986	0.014 ± 0.005			ps
Dendi	50	0.990	0.010 ± 0.009			5
Southern populations						
Fon	50	0.970 ± 0.017	0.020 ± 0.014	0.010 ± 0.009		5
AK1		AK1*1				
Northern populations						
Bariba	50	1.000				5
Berba	285	1.000				ps
Dendi	50	1.000				5
Southern populations						
Fon	50	1.000				5
CA2		CA2*1	CA2*2			
Northern populations						
Bariba	50	0.860	0.140 ± 0.035			5
Berba	284	0.856	0.144 ± 0.015			ps
Dendi	50	0.920	0.080 ± 0.027			5
Southern populations						
Fon	50	0.860	0.140 ± 0.035			5
ESD		ESD*1	ESD*2			
Northern populations						
Bariba	50	0.930	0.070 ± 0.025			5
Berba	285	0.951	0.049 ± 0.009			ps
Dendi	50	0.920	0.080 ± 0.027			5
Southern populations						
Fon	50	0.980	0.020 ± 0.014			5
Tofinu	100	0.935	0.065 ± 0.017			2
South	31	0.903	0.097 ± 0.038			3
GLO1		GLO1*1	GLO1*2			
Northern populations						
Bariba	50	0.340 ± 0.047	0.660			5
Berba	285	0.312 ± 0.019	0.688			ps
Dendi	50	0.340 ± 0.047	0.660			5
Southern populations						
Fon	50	0.350 ± 0.048	0.650			5
South	89	0.303 ± 0.034	0.697			3
PGD		PGD*A	PGD*C			
Northern populations						
Bariba	50	0.969	0.031 ± 0.017			5
Berba	285	0.916	0.084 ± 0.012			ps
Dendi	50	0.920	0.080 ± 0.027			5

(continued)

APPENDIX D. *(Continued)*

Populations and systems	N	Allele frequencies ± 1 SE				References[2]
Southern populations						
Fon	50	0.980	0.020 ± 0.014			5
Tofinu	101	0.941	0.059 ± 0.017			2
South	103	0.995	0.005 ± 0.005			3
PGM1		PGM1*1	PGM1*2			
Northern populations						
Bariba	50	0.850	0.150 ± 0.036			5
Berba	284	0.852	0.148 ± 0.015			ps
Dendi	50	0.760	0.240 ± 0.043			5
Southern populations						
Fon	50	0.860	0.140 ± 0.037			5
Tofinu	103	0.820	0.180 ± 0.027			2
South	105	0.800	0.200 ± 0.028			3
PGM1		PGM1*1A	PGM1*1B	PGM1*2A	PGM1*2B	
Northern populations						
Bariba	50	0.790 ± 0.041	0.060 ± 0.024	0.110 ± 0.031	0.040 ± 0.020	5
Berba	284	0.773 ± 0.018	0.079 ± 0.011	0.129 ± 0.014	0.019 ± 0.006	ps
Dendi	50	0.680 ± 0.047	0.070 ± 0.025	0.150 ± 0.036	0.100 ± 0.030	5
Southern populations						
Fon	50	0.660 ± 0.047	0.200 ± 0.040	0.090 ± 0.029	0.050 ± 0.022	5
PGM2		PGM2*1				
Northern populations						
Bariba	50	1.000				5
Berba	285	1.000				ps
Dendi	50	1.000				5
Southern populations						
Fon	50	1.000				5
HP		HP*1	HP*2			
Northern populations						
Berba	230	0.731	0.269 ± 0.022			ps
Southern populations						
Djedje	41	0.639	0.361 ± 0.057			2
Fon	71	0.657	0.343 ± 0.047			2
Goun	165	0.653	0.347 ± 0.045			2
Nago	76	0.688	0.312 ± 0.062			2
Tofinu	87	0.638	0.362 ± 0.041			2
South	412	0.643	0.357 ± 0.020			1
South	248	0.653	0.347 ± 0.025			4

[1] South: these samples include individuals of different populations of southern Benin.
[2] ps: present study; 1: Spedini et al., 1973; 2: Spedini et al., 1980; 3: Spedini et al., 1981b; 4: Spedini and Cresta, 1968; 5: Rickards and Martínez-Labarga, 1994.

APPENDIX E. *Allele and haplotype frequencies in the sub-Sahara African populations included in the correspondence analysis*

Populations and linguistic affiliation (stock, subfamily)	CDE	CDe	Cde	cDE	cDe	cde	ABO*A	ABO*B	MS	Ms	NS	HP*1	ACP1*A	ACP1*C	ACP1*R	AK1*2	PGM1*2	PGM1*6	PGD*C	PGD*R	PGM2*2	PGM2*6	Ref.[1]
Bushmen–Hottentots																							
Naron (Southern Africa) [Khoisan, Bushman]	0.000	0.017	0.000	0.007	0.901	0.075	0.161	0.013	0.155	0.505	0.000	0.388	0.208	0.000	0.236	0.069	0.026	0.000	0.009	0.000	0.035	0.000	1
Nama (Southern Africa) [Khoisan, Bushman]	0.000	0.118	0.000	0.056	0.744	0.081	0.246	0.171	0.205	0.455	0.050	0.594	0.164	0.003	0.218	0.038	0.163	0.034	0.003	0.003	0.004	0.000	2
G/wi (Southern Africa) [Khoisan, Bushman]	0.000	0.021	0.000	0.016	0.963	0.000	0.194	0.022	0.092	0.489	0.048	0.315	0.292	0.011	0.331	0.062	0.156	0.000	0.010	0.000	0.053	0.000	3
G//ana (Southern Africa) [Khoisan, Bushman]	0.000	0.010	0.000	0.125	0.865	0.000	0.032	0.031	0.192	0.507	0.037	0.302	0.469	0.000	0.235	0.062	0.180	0.000	0.048	0.000	0.060	0.000	4
!Kung (Southern Africa) [Khoisan, Bushman]	0.000	0.042	0.000	0.003	0.827	0.130	0.244	0.023	0.091	0.433	0.025	0.318	0.217	0.000	0.218	0.043	0.024	0.001	0.000	0.000	0.023	0.000	5
Pygmies																							
Babinga (C. A. R.)	0.000	0.000	0.044	0.006	0.829	0.114	0.162	0.102	0.226	0.322	0.184	0.386	0.062	0.000	0.167	0.000	0.138	0.000	0.018	0.000	0.001	0.060	6
Negroes																							
Bedik or Bassari (Senegal) [Nigritic, Atlantic]	0.002	0.016	0.000	0.079	0.632	0.268	0.203	0.230	0.099	0.429	0.178	0.725	0.257	0.000	0.003	0.000	0.181	0.000	0.048	0.000	0.001	0.000	7
Ambo or Ovambo (Namibia) [Nigritic, Bantoid]	0.000	0.074	0.000	0.130	0.757	0.038	0.158	0.171	0.108	0.429	0.122	0.695	0.195	0.004	0.028	0.000	0.188	0.000	0.046	0.001	0.006	0.000	8
Bantu (Transkei) [Nigritic, Bantoid]	0.000	0.051	0.000	0.109	0.658	0.182	0.243	0.123	0.179	0.464	0.069	0.454	0.148	0.000	0.000	0.025	0.164	0.000	0.109	0.000	0.000	0.000	9
Dama or Damara (S.W.A.) [Nigritic, Bantoid]	0.000	0.035	0.000	0.071	0.673	0.152	0.099	0.272	0.049	0.404	0.091	0.644	0.190	0.005	0.005	0.088	0.248	0.000	0.017	0.013	0.000	0.000	10
Hutu (Burundi) [Nigritic, Bantoid]	0.000	0.079	0.000	0.031	0.750	0.140	0.192	0.119	0.245	0.281	0.116	0.567	0.124	0.014	0.002	0.006	0.186	0.000	0.049	0.002	0.001	0.007	11
Njinga or Ngola (Angola) [Nigritic, Bantoid]	0.000	0.089	0.025	0.077	0.714	0.095	0.156	0.127	0.083	0.473	0.073	0.682	0.193	0.000	0.000	0.005	0.151	0.000	0.083	0.000	0.027	0.000	12
Nyaturu (Tanzania) [Nigritic, Bantoid]	0.000	0.075	0.000	0.047	0.760	0.118	0.174	0.112	0.162	0.371	0.093	0.582	0.153	0.000	0.000	0.005	0.160	0.003	0.034	0.000	0.000	0.000	13
Sango (C.A.R.) [Nigritic, Eastern]	0.000	0.030	0.000	0.081	0.717	0.173	0.179	0.120	0.175	0.453	0.031	0.705	0.226	0.000	0.048	0.013	0.164	0.000	0.021	0.000	0.000	0.000	14
Yoruba (Nigeria) [Nigritic, Kwa]	0.000	0.049	0.033	0.011	0.680	0.228	0.148	0.188	0.052	0.411	0.053	0.686	0.182	0.000	0.045	0.000	0.237	0.002	0.055	0.000	0.005	0.000	15
Berba (Benin) [Nigritic, Voltaic]	0.012	0.061	0.014	0.071	0.605	0.237	0.107	0.220	0.126	0.425	0.120	0.731	0.211	0.000	0.014	0.000	0.148	0.000	0.084	0.000	0.000	0.000	p.s.
Hadza (Tanzania) [Hamitic, Cushitic]	0.000	0.010	0.000	0.059	0.795	0.137	0.406	0.030	0.163	0.448	0.104	0.609	0.121	0.014	0.000	0.000	0.247	0.000	0.000	0.003	0.023	0.000	16
Mbugu (C.A.R.) [Hamitic, Cushitic]	0.000	0.042	0.000	0.042	0.687	0.229	0.190	0.111	0.181	0.331	0.100	0.654	0.223	0.000	0.043	0.019	0.075	0.000	0.034	0.000	0.000	0.000	17
Sandawe (Tanzania) [Khoisan, Sandawe]	0.000	0.035	0.000	0.051	0.707	0.207	0.171	0.129	0.283	0.313	0.043	0.639	0.157	0.000	0.000	0.007	0.191	0.000	0.055	0.005	0.007	0.000	13
Sara (Chad) [Sudanic, Central]	0.000	0.087	0.000	0.104	0.569	0.222	0.179	0.285	0.041	0.480	0.075	0.511	0.178	0.001	0.041	0.000	0.184	0.000	0.019	0.000	0.004	0.000	18

[1] 1: Jenkins et al., 1971; Jenkins and Corfield, 1972; Jenkins and Nurse, 1974; Nurse et al., 1977; 2: Jenkins and Corfield, 1972; Jenkins and Nurse, 1974; Roychoudhury and Nei, 1988; 3–4: Jenkins et al., 1975; Jenkins and Nurse, 1974; the AK1*2 allele frequency was calculated as a mean value of the Bushmen populations quoted in Jenkins et al., 1971, and Nurse et al., 1977; 5: Jenkins et al., 1971; Jenkins and Corfield, 1972; Jenkins and Nurse, 1974; Nurse et al., 1977; Roychoudhury and Nei, 1988; 6: Cavalli-Sforza et al., 1969; Santachiara-Benerecetti et al., 1980; the PGD allele frequencies refer to AKA Pygmies quoted in Vergnes et al., 1979; 7: Bouloux et al., 1972; 8: Nurse et al., 1987; 9: Creen et al., 1990; 10: Nurse et al., 1976; 11: Fraser et al., 1966; Giblett et al., 1966; Le Gall et al., 1982; 12: Nurse et al., 1979; 13: Godber et al., 1976; 14: Spedini et al., 1981a, 1982, 1983; 15: Blumberg et al., 1961; Mourant et al., 1976; Ojikutu et al., 1977; 16: Tills et al., 1982; 17: Spedini et al., 1981a, 1982, 1983; 18: Hiernaux, 1976; ps: present study.